

# A new arboreal microhylid frog of the genus *Anodonthyla* from south-eastern Madagascar

(Amphibia, Microhylidae)

Frank Glaw & Miguel Vences

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We describe a new species of *Anodonthyla* from the Ranomafana region in south-eastern Madagascar. *Anodonthyla moramora*, spec. nov. is the smallest *Anodonthyla* known so far, with adult snout-vent lengths of 15-16.5 mm in males and females. The new species is morphologically closest to *A. boulengeri* Müller which occurs syntopically at Ranomafana; however, among other characters *A. moramora* is distinguished by its smaller size, slower note repetition rate in advertisement calls and a strong genetic differentiation as indicated by a pairwise uncorrected sequence divergence of 11-12 % in a fragment of the mitochondrial 12S rRNA gene. For comparative reasons we also provide measurements of the holotypes of *Anodonthyla boulengeri*, *A. nigrigularis* Glaw & Vences and *A. rouxae* Guibé, and designate a lectotype for *Anodonthyla montana* Angel. The discovery of the new species described herein, and of a second genetically distinct form from Ranomafana, provide further support for a center of diversity and endemism of *Anodonthyla* in the south-east of Madagascar.

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## Introduction

Frogs of the genus *Anodonthyla* Müller, 1892 are conspicuous among the cophyline microhylids of Madagascar in having their center of diversity and endemism in south-eastern rather than northern Madagascar. Within the cophyline radiation (Andreone et al. 2005), which currently contains about 40 species in seven genera, at least 14 species and two genera (*Rhombophryne* and *Cophyla*) are so far only known from northern Madagascar (Glaw & Vences 1994). In contrast, records of *Anodonthyla* from the north (Blommers-Schlösser & Blanc 1991, Raxworthy et al. 1998) turned out to be misidentifications (Vences et al. 2002).

*Anodonthyla* currently contains four species, of which three, *A. montana* Angel, 1925, *A. nigrigularis* Glaw & Vences, 1992 and *A. rouxae* Guibé, 1974, are restricted to localities in south-eastern Madagascar. *Anodonthyla boulengeri* Müller, 1892 is widely distributed in eastern Madagascar, being relatively common at coastal low and mid-altitude localities (Glaw & Vences 1994). *Anodonthyla* are mainly arboreal frogs that breed in tree-holes or other water-filled cavities such as bamboo trunks. Only *A. montana*, a species specialized to high-altitude areas of the Andringitra mountains above the tree line, breeds in small pools in the granitic rocks (Blommers-Schlösser & Blanc 1991). As other cophylines, *Anodonthyla* have non-feeding tadpoles and exhibit



Fig. 1. *Anodonthyla moramora*, spec. nov. in life from Vohiparara, south-eastern Madagascar.

parental care (Blommers-Schlösser 1975).

Here we report on the discovery of a new small species of *Anodonthyla* that occurs sympatrically with *A. boulengeri* in the Ranomafana area in south-eastern Madagascar.

### Materials and Methods

Specimens were collected at night by locating calling males, or during the day by opportunistic searching of tree holes. They were euthanised by immersion in chlorobutanol solution, fixed in 90 % ethanol and preserved in 70 % ethanol. Tissue samples were preserved separately in 99 % ethanol. Specimens were deposited in the collections of the Université d'Antananarivo, Département de Biologie Animale (UADBA), Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn (ZFMK), Zoological Museum Amsterdam (ZMA) and Zoologische Staatssammlung München (ZSM). Furthermore we studied specimens from the Museum National d'Histoire Naturelle, Paris (MNHN), the Naturhistorisches Museum Basel (NMBA), and the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (SMF).

DNA was extracted and a section of the mitochondrial 12S rRNA gene amplified and sequenced using standard protocols and primers (Vences et al. 2000). The sequences were aligned by hand and contained a total of 372 positions. Hypervariable regions as well as posi-

tions with indels in one or more taxa were excluded. The data set was analyzed using the program PAUP\*, version 4b10 (Swofford 2002). We performed maximum likelihood heuristic searches with 100 random addition sequence replicates. The substitution model for maximum likelihood analyses was determined using Modeltest (Posada & Crandall 1998) which selected a Tamura-Nei (TrN) model with empirical base frequencies (freqA = 0.3173, freqC = 0.2748; freqG = 0.1832; freqT = 0.2247) and substitution rates (rate[A-G] = 3.6327; [C-T] = 7.2033; other rates = 1) and a gamma distribution shape parameter of 0.2211 as best fitting the data. In addition we performed bootstrap analyses (2000 replicates) under the maximum likelihood and maximum parsimony optimality criteria. DNA sequences were deposited in Genbank; voucher specimens and accession numbers are as follows: *Scaphiophryne calcarata* (Isalo; ZSM 118/2002; AY594051); *Platypelis grandis* (Mantady; ZSM 162/2002; AY594026); *Platypelis barbouri* (Andasibe; ZSM 1/2002; AY594022); *Cophyla phyllodactyla* (Nosy Be; ZSM 460/2000; AY684184); *Anodonthyla boulengeri* (Ilampy; Field number of F. Andreone, No. 10243; AY684182); *A. boulengeri* (Foulpointe; ZSM 264/2002; AY594015); *A. montana* (Andringitra; UADBA-MV 2001.530; AY594014); *A. moramora* (Vohiparara; UADBA 20690; AY684183); *A. sp.* (Ranomafana; ZSM 673/2003; AY594016).

The following morphological measurements were taken by M.V. to the nearest 0.1 mm using a caliper: Snout-vent length, SVL; maximum head width (HW);

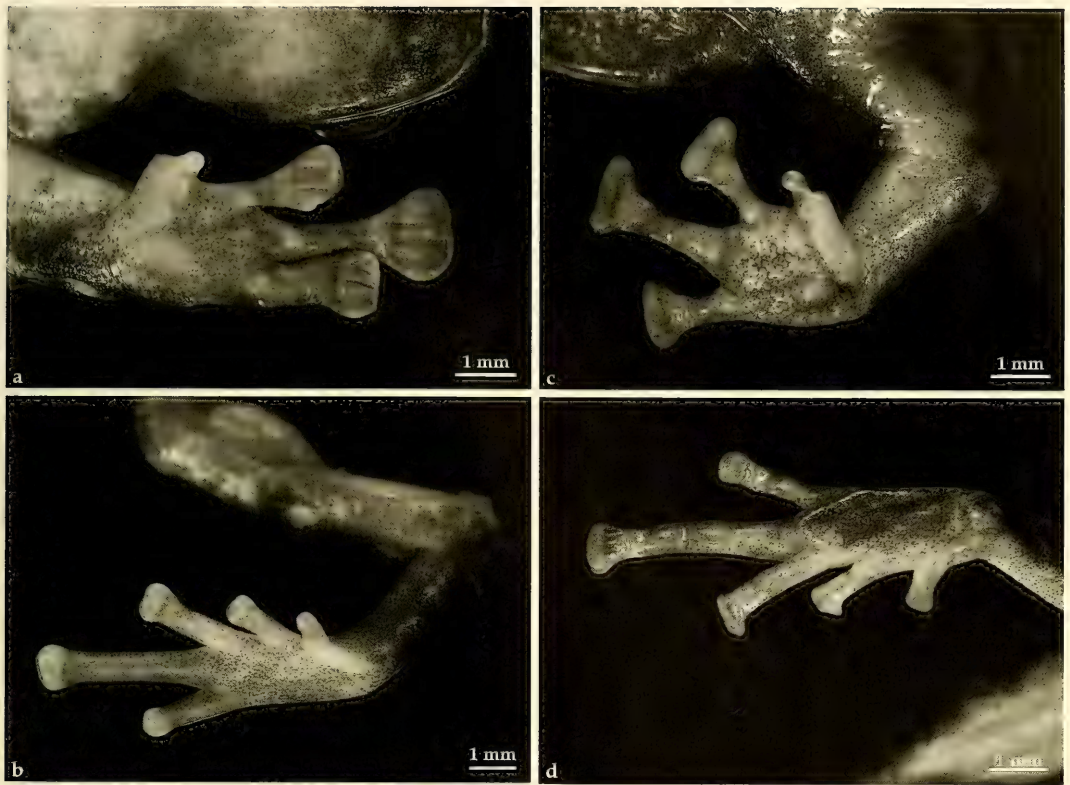


Fig. 2. Ventral view of hand and foot of a male of *Anodonthyla boulengeri* Müller (a and b; ZSM 264/2002) in comparison with a male of *A. moramora*, spec. nov. (c and d; paratype ZFMK 62308).

head length from tip of snout to posterior edge of snout opening (HL); horizontal tympanum diameter (TD); horizontal eye diameter (ED); distance between anterior edge of eye and nostril (END); distance between nostril and tip of snout (NSD); distance between both nostrils (NND); forelimb length, from limb insertion to tip of longest finger (FORL); hand length, to the tip of the longest finger (HAL); hindlimb length, from the cloaca to the tip of the longest toe (HIL); tibia length (TIBL); foot length including tarsus (FOTL); foot length (FOL), prepollex length from the tip of the prepollex to the proximal extreme of what could be recognized as a distinct morphological unit (PREP). Calls were recorded with portable tape recorders with external microphones. They were analyzed on the sound analyzing system MEDAV Spektro 3.2.

*Anodonthyla moramora*, spec. nov.  
Figs 1-2

**Types.** Holotype: ZSM 744/2003, adult male, collected by F. Glaw, M. Puente, M. Thomas, L. Raharivololoniaina and D. R. Vieites on 20 January 2003 next to Kido-nafo bridge, Vohiparara near Ranomafana, south-

eastern Madagascar (21°13' S, 47°22' E, ca. 1000 m above sea level). – Paratypes: ZSM 705/2003, ZSM 706/2003 and ZMA 19428-19429, four adult males with same collecting data as holotype; UADBA 20686, adult specimen of undetermined sex with same collecting data as holotype; UADBA 20690, adult male collected by same collectors as holotype on 16 January 2003 in Ranomafana National Park; ZFMK 62275-62276, two males collected by F. Glaw, D. Rakotomalala and F. Ranaivojaona on 3-4 March 1996 at the same locality as the holotype, ZFMK 62308-62309, one male and one female, collected by F. Glaw, D. Rakotomalala and F. Ranaivojaona on 2 March 1996 in the Ranomafana National Park.

**Diagnosis and comparisons.** Assigned to the genus *Anodonthyla* based on the distinct prepollex visible in male specimens (Fig. 2), and on molecular phylogenetic relationships (see below). This species is distinguished from *Anodonthyla montana* and *A. rouxae* by a much smaller size (SVL of adult males 15-16.5 mm vs. 24-40 mm). Furthermore, it differs from both species by its relative toe length (third toe longer than fifth vs. fifth longer than third or both toes of similar length), and from *A. rouxae* by absence of a distinct supratympanic fold (vs. presence). The

new species is distinguished from *A. nigrigularis* by its smaller size (SVL of adult males 15-16.5 mm vs. 21-24 mm), lack of dark pigmentation on the vocal sac, and slower call repetition rate in advertisement calls (0.6-0.9 vs 1.0-1.4 notes per second). Morphologically the new species is most similar to *A. boulengeri*, but is distinguished by a smaller size (SVL of adult males 15-16.5 mm vs. 16-22 mm), by often presenting greenish dorsal colouration in life (vs. absence of greenish tones), by a much slower call repetition rate (0.6-0.9 vs 1.8-3.1 notes per second; Figs. 3-4), and by a strong genetic differentiation (11-12 % uncorrected pairwise sequence divergence in the sequenced 12S rDNA fragment).

### Description of holotype

Specimen in excellent state of preservation. SVL 15.9 mm (for other measurements see tab. 1). Body slender; head as wide as long, not wider than body; snout rounded in dorsal and lateral views; nostrils directed laterally, moderately protuberant, slightly nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region straight; tympanum indistinct, rounded, about half of eye diameter; supratympanic fold absent; tongue ovoid, posteriorly broader than anteriorly, free and not notched or forked; small maxillary teeth present; vomerine teeth absent; choanae rounded. Arms slender; sub-articular tubercles not recognizable; outer metacar-

**Tab. 1.** Morphometric measurements (all in mm) of types and comparative specimens of *Anodonthyla moramora* and *A. boulengeri*, and name-bearing types of *A. nigrigularis*, *A. rouxae* and *A. montana*. For abbreviations of measured variables, see Materials and Methods; further abbreviations used: M (male); HT (holotype); PT (paratype), LT (lectotype). RHL (relative hindlimb length) is coded as follows: Tibiotarsal articulation reaches 1, forelimb insertion; 2, between forelimb insertion and tympanum; 3, tympanum; 4, between tympanum and eye; 5, posterior eye corner; 6, eye center; 7, anterior eye corner. The holotype of *A. boulengeri* was described from "Madagascar" without precise locality data. The specimen SMF 4299, marked with an asterisk, is the holotype of *Mantella pollicaris* Boettger, 1913, junior synonym of *Anodonthyla boulengeri*.

|                        | Number        | Locality             | Sex | Status | SVL  | HW   | HL   | TD    | ED  | END | NSD |
|------------------------|---------------|----------------------|-----|--------|------|------|------|-------|-----|-----|-----|
| <i>A. moramora</i>     | ZFMK 62308    | Ranomafana Nat. Park | M   | PT     | 16.0 | 5.2  | 5.2  | 1.0   | 1.8 | 1.1 | 0.9 |
|                        | ZFMK 62275    | Vohiparara           | M   | PT     | 15.9 | 5.0  | 5.0  | 1.2   | 1.5 | 1.3 | 1.0 |
|                        | ZFMK 62276    | Vohiparara           | M   | PT     | 15.1 | 5.0  | 5.0  | 1.2   | 1.5 | 1.2 | 1.0 |
|                        | ZFMK 62309    | Ranomafana Nat. Park | F   | PT     | 15.4 | 5.0  | 4.8  | 0.9   | 1.7 | 1.0 | 1.0 |
|                        | ZMA 19428     | Vohiparara           | M   | PT     | 15.8 | 5.0  | 5.2  | 1.1   | 1.6 | 1.0 | 1.0 |
|                        | ZMA 19429     | Vohiparara           | M   | PT     | 16.0 | 5.0  | 5.2  | 1.0   | 1.6 | 0.9 | 1.0 |
|                        | ZSM 705/2003  | Vohiparara           | M   | PT     | 15.0 | 5.0  | 5.0  | 1.1   | 2.0 | 1.1 | 0.9 |
|                        | ZSM 706/2003  | Vohiparara           | M   | PT     | 16.5 | 5.5  | 5.4  | 1.1   | 2.0 | 1.1 | 1.0 |
|                        | ZSM 744/2003  | Vohiparara           | M   | HT     | 15.9 | 5.0  | 5.0  | 1.1   | 2.0 | 1.2 | 1.1 |
| <i>A. boulengeri</i>   | NMBA 1448     | unknown (Madagascar) | F   | HT     | 20.3 | 6.6  | 6.4  | 1.0   | 2.1 | 1.4 | 1.4 |
|                        | SMF 4299      | Anevoka              | F   | HT*    | 21.2 | 6.2  | 6.1  | 1.5   | 2.3 | 1.3 | 1.0 |
|                        | ZFMK 52775    | Nosy Mangabe         | M   |        | 22.0 | 7.5  | 6.4  | [1.3] | 2.7 | 1.5 | 1.1 |
|                        | ZFMK 52781    | Nosy Mangabe         | M   |        | 21.9 | 7.0  | 6.3  | [1.5] | 2.4 | 1.6 | 1.2 |
|                        | ZFMK 52783    | Nosy Mangabe         | M   |        | 18.0 | 5.7  | 5.7  | -     | 2.0 | 1.3 | 0.9 |
|                        | ZFMK 52782    | Nosy Mangabe         | M   |        | 22.3 | 7.0  | 6.5  | [1.5] | 2.1 | 1.5 | 1.0 |
|                        | ZFMK 53742    | Andasibe             | M   |        | 19.0 | 5.9  | 5.6  | 1.3   | 1.7 | 1.3 | 1.0 |
|                        | ZFMK 52780    | Andasibe             | F   |        | 19.4 | 5.7  | 5.8  | 1.4   | 1.9 | 1.5 | 1.1 |
|                        | ZFMK 62215    | Andasibe             | M   |        | 17.8 | 5.8  | 5.5  | 1.2   | 2.0 | 1.6 | 1.0 |
|                        | ZFMK 62222    | Andasibe             | M   |        | 16.2 | 5.3  | 5.4  | 1.0   | 1.6 | 1.0 | 0.7 |
|                        | ZFMK 52784    | Nosy Boraha          | M   |        | 15.7 | 5.1  | 5.2  | 1.0   | 1.6 | 1.3 | 1.0 |
|                        | ZFMK 52786    | Nosy Boraha          | M   |        | 17.3 | 5.5  | 5.5  | 0.9   | 1.9 | 1.3 | 1.0 |
|                        | ZFMK 52785    | Nosy Boraha          | F   |        | 19.2 | 5.7  | 5.7  | 1.1   | 2.2 | 1.3 | 0.9 |
|                        | ZFMK 62313    | Ranomafana           | M   |        | 18.7 | 5.6  | 5.4  | 1.0   | 2.0 | 1.3 | 0.9 |
|                        | ZMA 19430     | Ranomafana           | M   |        | 17.3 | 5.0  | 4.6  | 0.9   | 2.0 | 1.2 | 1.0 |
|                        | ZSM 264/2002  | Foulpointe           | M   |        | 18.0 | 5.4  | 5.2  | 1.1   | 2.1 | 1.2 | 1.0 |
|                        | ZSM 642/2003  | Ranomafana           | M   |        | 17.4 | 5.0  | 5.3  | 1.1   | 2.0 | 1.3 | 0.8 |
| ZSM 643/2003           | Ranomafana    | F                    |     | 18.2   | 5.1  | 5.4  | 1.3  | 1.9   | 1.2 | 1.1 |     |
| <i>A. nigrigularis</i> | ZFMK 53745    | Nahampoana           | M   | HT     | 20.7 | 6.8  | 6.0  | 1.1   | 1.9 | 1.3 | 0.9 |
| <i>A. rouxae</i>       | MNHN 1973.666 | Chaînes Anosyennes   | M   | HT     | 28.3 | 9.2  | 8.6  | 1.3   | 3.0 | 2.0 | 1.6 |
| <i>A. montana</i>      | MNHN 1924.107 | Andringitra          | F   | LT     | 33.0 | 11.2 | 10.0 | 2.5   | 3.8 | 2.2 | 2.2 |

pal tubercle not distinct; prepollex large and distinct, extending from the area generally occupied by the inner metacarpal tubercle to the tip of first finger; fingers without webbing; relative length of fingers  $1 < 2 < 4 < 3$ , fourth finger slightly longer than second; finger disks distinctly enlarged, of triangular shape; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaching the eye center when hindlimb adpressed along body; tibia length 46 % of SVL; lateral metatarsalia strongly connected; metatarsal tubercles not recognizable; no webbing between toes; relative length of toes  $1 < 2 < 5 < 3 < 4$ ; third toe distinctly longer than fifth. Skin on dorsum smooth, with a row of indistinct, large dorsolateral tubercles. Ventral skin smooth.

After 10 months in preservative, dorsum light grey-brown with well-delimited symmetrical darker markings: one W-shaped marking on anterior dorsum, an inverse V-shaped marking on posterior dorsum. Surface of head dark brown except a narrow light brown stripe between the eyes. Dark brown patches are also present above the tympanum. The ventral side is uniformly cream.

| NND | FORL | HAL | HIL  | FOTL | FOL  | TIBL | PREP | RHL |
|-----|------|-----|------|------|------|------|------|-----|
| 1.7 | 10.7 | 5.0 | 24.1 | 11.0 | 6.8  | 7.6  | 1.6  | 5   |
| 1.5 | 20.0 | 4.3 | 22.5 | 10.2 | 6.7  | 7.0  | 1.6  | 6   |
| 1.6 | 10.2 | 4.5 | 22.2 | 10.0 | 6.6  | 7.3  | 1.5  | 5   |
| 1.7 | 10.4 | 4.3 | 22.8 | 10.5 | 6.6  | 7.2  | —    | 6   |
| 1.9 | 10.1 | 4.9 | 23.0 | 10.2 | 6.4  | 7.2  | 1.9  | 3   |
| 1.9 | 9.5  | 4.9 | 22.3 | 11.0 | 6.7  | 7.2  | 1.6  | 4   |
| 1.8 | 9.7  | 4.5 | 22.2 | 10.0 | 6.1  | 7.2  | 1.9  | 6   |
| 2.0 | 10.4 | 5.0 | 24.4 | 10.7 | 6.6  | 7.5  | 1.7  | 5   |
| 1.8 | 10.4 | 5.0 | 23.2 | 10.6 | 6.8  | 7.3  | 1.8  | 6   |
| 1.8 | 12.7 | 5.5 | 27.3 | 12.1 | 7.7  | 9.9  | —    | 3   |
| 2.2 | 12.6 | 5.3 | 29.2 | 13.0 | 8.4  | 9.5  | —    | 3   |
| 2.0 | 14.6 | 6.8 | 32.1 | 14.5 | 9.1  | 10.0 | 1.8  | 3   |
| 2.3 | 14.0 | 6.8 | 30.5 | 14.1 | 9.0  | 9.8  | 1.6  | 3   |
| 1.6 | 12.0 | 5.6 | 27.1 | 12.1 | 7.7  | 8.6  | 1.6  | 5   |
| 2.2 | 12.0 | 6.4 | 31.0 | 14.2 | 9.1  | 9.7  | 1.7  | 3   |
| 1.7 | 10.5 | 5.4 | 25.6 | 11.5 | 7.1  | 8.3  | 1.4  | 3   |
| 1.6 | 11.6 | 5.4 | 27.7 | 12.6 | 8.0  | 8.5  | —    | 3   |
| 1.8 | 10.6 | 5.1 | 27.5 | 12.6 | 8.0  | 8.5  | 1.7  | 6   |
| 1.6 | 11.1 | 4.7 | 25.3 | 11.5 | 7.3  | 8.3  | 1.6  | 5   |
| 1.7 | 9.4  | 4.1 | 21.0 | 9.6  | 6.4  | 6.9  | 1.2  | 3   |
| 1.9 | 11.2 | 5.3 | 24.2 | 11.1 | 6.8  | 7.5  | 1.4  | 3   |
| 1.8 | 10.6 | 4.4 | 24.9 | 10.4 | 6.3  | 7.7  | —    | 3   |
| 1.7 | 11.2 | 5.2 | 28.3 | 12.8 | 8.0  | 8.8  | 1.6  | 5   |
| 1.8 | 11.3 | 5.0 | 26.9 | 12.0 | 7.6  | 8.2  | 1.7  | 5   |
| 1.9 | 11.6 | 4.9 | 24.6 | 11.3 | 7.3  | 7.8  | 1.6  | 3   |
| 1.8 | 11.4 | 5.0 | 26.7 | 11.7 | 7.2  | 9.2  | 1.5  | 7   |
| 1.5 | 13.2 | 5.4 | 29.6 | 13.2 | 8.2  | 8.9  | —    | 6   |
| 2.2 | 13.0 | 6.2 | 31.4 | 14.0 | 9.0  | 9.8  | 1.8  | 3   |
| 3.0 | 17.8 | 9.2 | 40.2 | 20.0 | 13.1 | 11.5 | 2.0  | 2   |
| 3.4 | 19.4 | 8.9 | 41.6 | 20.3 | 13.3 | 13.4 | —    | 1   |

Colour in life. Based on colour slides of four specimens. The general pattern is similar to that in preservative. Dorsal surface light beige to green-brown, with three or four symmetrical dark brown markings across the back: one bar between the posterior parts of the eyes, one V- or W-shaped marking on the anterior dorsum (can be reduced), one more or less angular and irregularly shaped bar on the posterior dorsum that is continued on the tibia, and one further bar before the cloaca which can be reduced to two isolated spots. Ventral side olive green or light grey, especially on the ventral surface of limbs, fingers and toes. Chest dark grey. The whole ventral surface can have fine whitish dots.

Variation. Measurements of eight paratypes are given in tab. 1 (UADBA specimens were not available for direct comparison). They all agree largely with the holotype in morphology. The single female specimen (ZFMK 62309) was of similar size to the male specimens; its SVL (15.4 mm) was 98 % of the mean male SVL in our sample (15.8 mm). The paratypes ZSM 705/2003 and 706/2003 have one forelimb removed for DNA sampling. This is also the case for ZMA 19428-19429 which additionally have been dissected and part of the inner organs removed for karyological analysis.

**Etymology.** The specific name is derived from the Malagasy expression "mora mora", meaning slowly or calmly. It refers to the slow call repetition rate of the new species. The name is used as noun in apposition.

**Distribution.** *Anodonthyla moramora* is hitherto only known from the Ranomafana region, from Ranomafana village (ca. 550 m a. s. l.) to the Kidonafo bridge near Vohiparara (1000 m a. s. l.).

**Natural history.** Calling males were observed mostly after dusk in primary rain forest and secondary vegetation. They were sitting on tree trunks, the head oriented upwards, at heights of 50-150 cm above the ground. Other calling males were located before dusk in small tree holes or hidden under extensive moss layers on tree trunks. Calling activity was regularly heard in the months January, February and March, indicating an extended breeding period (at least) in the rainy season. The only female (ZFMK 62309) was found close to a calling male (ZFMK 62308) on a tree trunk before dusk. Close to Ranomafana village, *A. moramora* was found in acoustic syntopy with *A. boulengeri*.

**Advertisement calls.** Calls were recorded on 29 February 1996 at 21:00 h at 22 °C air temperature close to the Manja Hotel in Ranomafana. If highly motivated and undisturbed, specimens emitted long series, lasting several minutes, of regularly repeated

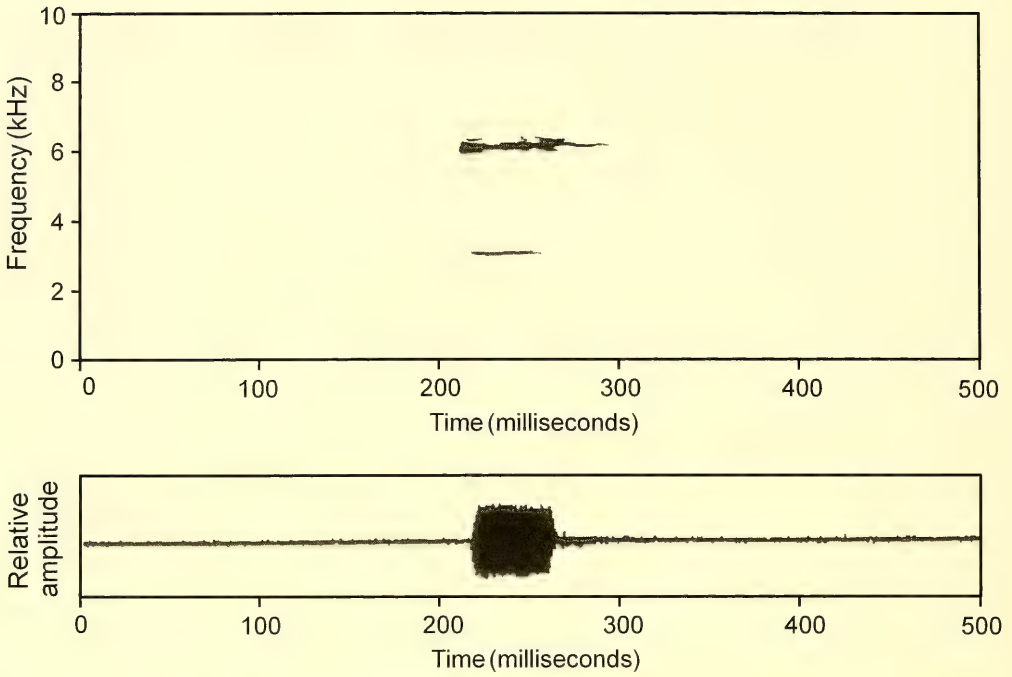


Fig. 3. Sonogram and oscillogram of a call of *Anodonthyla moramora*, spec. nov. recorded on 29 February 1996 at Ranomafana, at an air temperature of 22 °C.

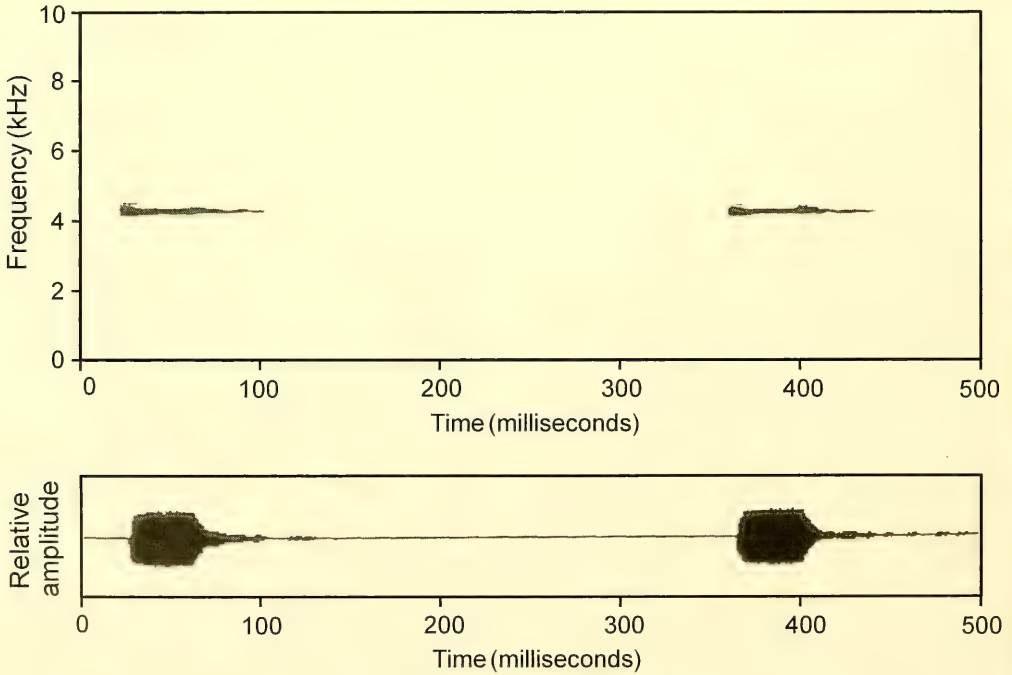


Fig. 4. Sonogram and oscillogram of a call of *Anodonthyla boulengeri* Müller, recorded on 29 February 1996 at Ranomafana, at an air temperature of 22 °C and in syntopy with *A. moramora*, spec. nov.

calls consisting of single melodious notes. Each note (Fig. 3) corresponds to one expiration. The vocal sac of calling males is strongly inflated during the vocalizations, but also in the silent intervals between two calls. The dominant frequency is 5400-6250 Hz, a second frequency band (fundamental frequency) is recognizable at 2700-3150 Hz. Depending on the conditions of recording and analysis, a weak harmonic exists at 8300 Hz. Temporal call parameters are given in tab. 2.

**Molecular differentiation and relationships.** After exclusion of 57 hypervariable or gapped positions, the dataset consisted of 315 characters of which 95 were variable. Maximum likelihood analysis recovered the tree shown in Fig. 5 in which all included *Anodonthyla* formed a monophyletic group to the exclusion of the other cophylines (*Platypelis* and *Cophyla*). *A. moramora* was sister to another specimen from Ranomafana which is likely to represent a further new species, while two analyzed *A. boulengeri* formed a second clade but were genetically quite different from each other (12 % uncorrected pairwise sequence divergence). *A. moramora* had 11-12 % pairwise sequence divergence to the two specimens

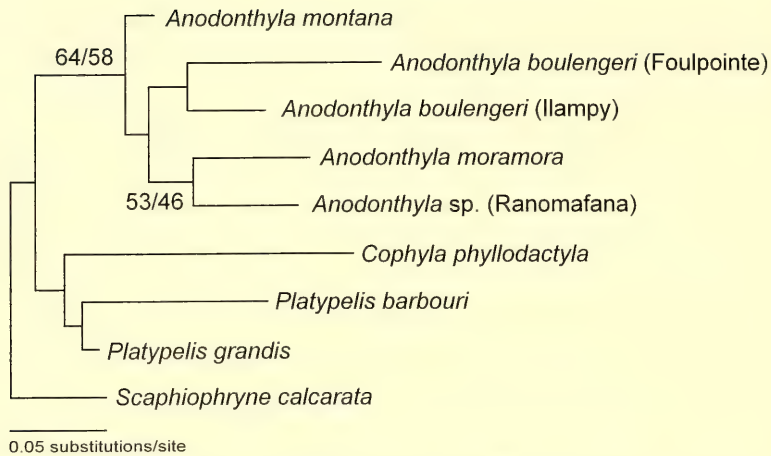
of *A. boulengeri*. *A. montana* occupied the most basal position among the *Anodonthyla* included in the molecular analysis.

**Other available names.** According to Blommers-Schlösser & Blanc (1991), *Mantella pollicaris* Boettger, 1913 is a junior synonym of *Anodonthyla boulengeri*, and therefore needs to be considered as possible earlier name for *Anodonthyla moramora*. The holotype of *M. pollicaris* is distinctly larger than *A. moramora*. The specimen was collected at Anevoka, eastern Madagascar. This locality which could not be located by Blommers-Schlösser & Blanc (1991) is on the way from Tamatave to Tanaramè (Boettger 1913: 273) and may correspond to a village with this name close to Andasibe (18°56'S, 48°28'E, 936 m a.s.l., <http://www.calle.com/world/>).

**Comparisons.** *Anodonthyla moramora* is morphologically most similar to *Anodonthyla boulengeri*. However, it shows a relatively consistent smaller size than that species, with only two out of 17 specimens of *A. boulengeri* being in the size range of *A. moramora* (Tab. 1). Furthermore, the greenish colouration that is typical for most specimens of

**Tab. 2.** Basic bioacoustic parameters among specimens of *Anodonthyla moramora*, *A. boulengeri* and *A. nigrigularis* recorded from different populations. Temporal measurements are given in milliseconds (ms) as range, with mean ± standard deviation in parentheses.

| Species                | Locality     | Recording date                   | Temperature<br>[°C] | Note duration<br>[ms]   | Inter-note<br>interval<br>duration<br>[ms] | Dominant<br>frequency<br>[Hz] | Call<br>repetition<br>rate<br>[notes/s] |
|------------------------|--------------|----------------------------------|---------------------|-------------------------|--|-------------------------------|---|
| <i>A. moramora</i>     | Ranomafana   | 29 February 1996,<br>19:20 h     | 22                  | 47-80<br>(66±11, N=27)  | 1468-2375<br>(1597±183, N=24)              | 5400-5700                     | 0.6-0.9                                 |
| <i>A. boulengeri</i>   | Nosy Mangabe | 12 March 1991                    | ca. 25              | 20-46<br>(35±7, N=17)   | 282-472<br>(370±50, N=15)                  | 3500-3750                     | 2.5                                     |
| <i>A. boulengeri</i>   | Nosy Mangabe | 12 March 1991                    | ca. 25              | 18-29<br>(22±3, N=12)   | 413-677<br>(482±80, N=11)                  | 3500-3700                     | 2.0                                     |
| <i>A. boulengeri</i>   | Nosy Boraha  | 4-7 March 1991                   | ca. 25              | 24-28<br>(26±2, N=7)    | 562-654<br>(611±39, N=6)                   | 4100-4300                     | 1.8                                     |
| <i>A. boulengeri</i>   | Nosy Boraha  | 4-7 March 1991                   | ca. 25              | 35-37<br>(37±1, N=7)    | 867-1064<br>(971±78, N=5)                  | –                             | –                                       |
| <i>A. boulengeri</i>   | Andasibe     | 30 January 1996,<br>17:45 h      | 22.5                | 49-55<br>(52±2, N=11)   | 268-389<br>(305±35, N=10)                  | 4200-4500                     | 2.6-2.9                                 |
| <i>A. boulengeri</i>   | Ankeniheny   | 18 February 1994,<br>21:00 h     | 22                  | 61-86<br>(72±8, N=13)   | 283-352<br>(313±17, N=12)                  | 4000-4200                     | 2.7                                     |
| <i>A. boulengeri</i>   | Ranomafana   | 29 February 1996,<br>19:20 h     | 22                  | 49-80<br>(65±11, N=16)  | 268-299<br>(283±9, N=14)                   | 4100-4350                     | 2.8-3.1                                 |
| <i>A. nigrigularis</i> | Nahampoana   | 4 January 1991                   | –                   | 60-117<br>(95±20, N=10) | 642-797<br>(694±51, N=8)                   | 4500                          | 1.3-1.4                                 |
| <i>A. nigrigularis</i> | Andohahela   | 1992 (recording<br>of D. Vallan) | –                   | 65-78<br>(69±4, N=14)   | 753-1014<br>(855±87, N=11)                 | 3600-3800                     | 1.0-1.1                                 |



**Fig. 5.** Maximum likelihood phylogram based on analysis of 319 base pairs of the 12S rRNA gene in species of *Anodonthyla* and other cophylines. The numbers above branches are bootstrap values (in percent) from maximum likelihood and maximum parsimony analysis (2000 replicates each; values below 50 % not shown).

*A. moramora* has never been observed in *A. boulengeri*, but unfortunately it quickly fades upon preservation. Although it is difficult to describe differences in prepollex shape in terms of clearly defined character states, it also is true that all male specimens of *A. moramora* examined had a more distinct prepollex than *A. boulengeri*, which is also reflected in prepollex length (Tab. 1). The best character to distinguish both species in the field is certainly the call which has a much slower repetition rate in *A. moramora* (Tab. 2). This is true in comparison of all populations of *A. boulengeri* examined so far, including those occurring syntopically with *A. moramora* in the Ranomafana region.

**Lectotype designation for *A. montana*.** From the four *Anodonthyla* species known to date, three (*A. boulengeri*, *A. nigrigularis* and *A. rouxae*) have been described based on holotype specimens, with additional specimens designated as paratypes. In contrast, *Anodonthyla montana* Angel, 1925 has been described based on a syntype series of four specimens (MNHN 1924.104-107), all from "Massif de l'Andringitra, où on les trouve à une altitude voisine de 2,600 mètres" and collected by Perrier de la Bâthie. Upon examination in December 2003, these four specimens were in a relatively poor state of preservation, of uniformly brown colour with the original pattern completely faded, and with a number of ventral and dorsal cuts made for dissection. MNHN 1924.105 and 1924.106 are subadult specimens of 24.0 and 24.8 mm SVL, while MNHN 1924.104 and 1924.107 are adult females (as visible by the presence of oocytes) of 35.7 and 33.0 mm SVL. To stabilize the name, we hereby designate the

specimen MNHN 1924.107, which is in slightly better state of preservation as MNHN 1924.104, as lectotype of *Anodonthyla montana* Angel, 1925.

## Discussion

The discovery and description of a new species of *Anodonthyla* at Ranomafana corroborates the south-eastern center of diversity of this genus. By recording the co-occurrence of *Anodonthyla moramora* and *A. boulengeri* at Ranomafana, we also provide the first reliable example of syntopy for two species of this genus. The molecular tree (Fig. 5) further provides evidence that another microhylid frog from Ranomafana (here named *Anodonthyla* sp.) belongs to this genus. Considering the relatively short DNA sequences analysed and the low bootstrap support of most nodes (Fig. 5), it has to be stressed that the phylogenetic relationships suggested by our tree are not reliable, and that the molecular data presented herein merely serve to demonstrate a strong genetic differentiation of the new species described. The strong genetic differentiation among the two individuals of *A. boulengeri* further demonstrates that this species may be composed of several cryptic, yet unrecognized species.

Despite intensive surveys in central-eastern rainforests around Andasibe and Moramanga, we have never seen or heard *Anodonthyla moramora* in this region. Therefore, we assume that it is a regional endemic for south-eastern Madagascar, where it probably occurs also at additional sites.

The new species is relatively common around Vohiparara, close to Ranomafana. It occurs within



the boundaries of Ranomafana National Park, and is therefore not to be considered as threatened. However, more inventory work is necessary to understand its actual distribution range and habitat requirements before a reliable statement can be made.

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